
THE ANDES: A GEOLOGICAL OVERVIEW FROM A BIOLOGICAL PERSPECTIVE

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ABSTRACT

Geological events of biological importance in the history of the Andes include their impact on global climates through an influence on atmospheric circulation, rainfall patterns, and the atmospheric concentration of CO₂; habitat diversification from lowlands through páramo to glaciated peaks; and migratory pathways ranging from discontinuous (mesic elements), highly discontinuous (páramo elements), barriers (to east-west migrations), to selective pathways (via the dry Andean valleys). The timing of these effects is a function of the uplift history of three (to nine) morphotectonic segments of the Andes resulting in (1) mostly lowland swamp and fluvial environments in the Cretaceous and Paleocene, (2) moderate uplands beginning in the Late Eocene (ca. 40 million years ago [Ma]), (3) appression of an offshore volcanic chain (the proto-Cordillera Occidental) in the Oligocene (ca. 30 Ma), (4) uplift of the proto-Cordillera Oriental and the Altiplano to about half their present altitude by the Middle Miocene (ca. 15 Ma), and (5) uplift of the remaining half within approximately the past 10 million years. The early appearance of a biological community recognizable as the Atacama Desert is estimated at ca. 15 Ma, and the beginnings of a páramo at ca. 3.5 Ma. Longer-term (Milankovitch) and shorter-term (Younger Dryas, Medieval warm/dry period, Little Ice Age, Heinrich, and Dansgaard-Oeschger [D-O]) climatic events, known initially from the high latitudes, are now widely recognized throughout Latin America, including the Andes. They document a dynamic physical environment from the Cretaceous through the Holocene and on all timescales.

Key words: Altiplano, Andes, Cretaceous, Eocene, Paleocene, páramo.

The Andes are one of the major physiographic features of the Earth. They are the longest mountain chain at nearly 9000 km and at the widest are 750 km in Bolivia. Only the Himalayas with Mount Everest (8848 m) are higher than the Andes with Cerro Aconcagua (6962 m; Fig. 1). Their geologic development over time (Cordani et al., 2000; Ramos & Aleman, 2000; Veblen et al., 2007) has modified global and regional climate by affecting atmospheric circulation and the distribution of rainfall, and by contributing larger or lesser amounts of CO₂ to the atmosphere, correlated with the waxing and waning of orogeny. More than 90% of the world's seismic energy is released at convergent margins (Oncken et al., 2006), and the Andean plate boundaries are a major outlet of this energy. The Andes also provide altitudinally zoned habitats from rainforest to páramo to glaciated peaks, an east-west differentiation into wetter and drier sides through rain shadow effects, a discontinuous north-south migratory pathway for mid-elevation mesic biotas, an even more discontinuous route for higher Andean and páramo elements, an east-west pathway for interchange of arid elements through the dry Andean valleys, and an extensive

range of edaphic diversity. Their rise during the Cretaceous and particularly in the Cenozoic also constituted a gradual but ultimately formidable vicariant event. The influence of altitudinal gradients on distribution patterns and evolutionary processes is complex, but a first step in achieving a better understanding of the relationship has been to recognize two categories of physical changes that occur with differences in altitude. One is altitude-specific, such as atmospheric pressure, temperature, and clear-sky turbidity (cloudiness). The other is more variable but, nonetheless, affects the first category: moisture, hours of sunshine, wind, season length, and edaphic factors. The distinction will be important eventually for more precisely modeling the effect of altitude on biotas, for example, like those on the Altiplano (Körner, 2007). Uplift of a feature of this magnitude is also affecting the CO₂ concentration of the atmosphere, and hence climates, by increased erosion of silicate rocks through chemical transformations, where, for example, wollastonite (CaSiO₃) is transformed to calcium carbonate (CaCO₃) and silicon dioxide (SiO₂) while capturing CO₂ from the atmosphere. The process runs in the direction of SiO₂

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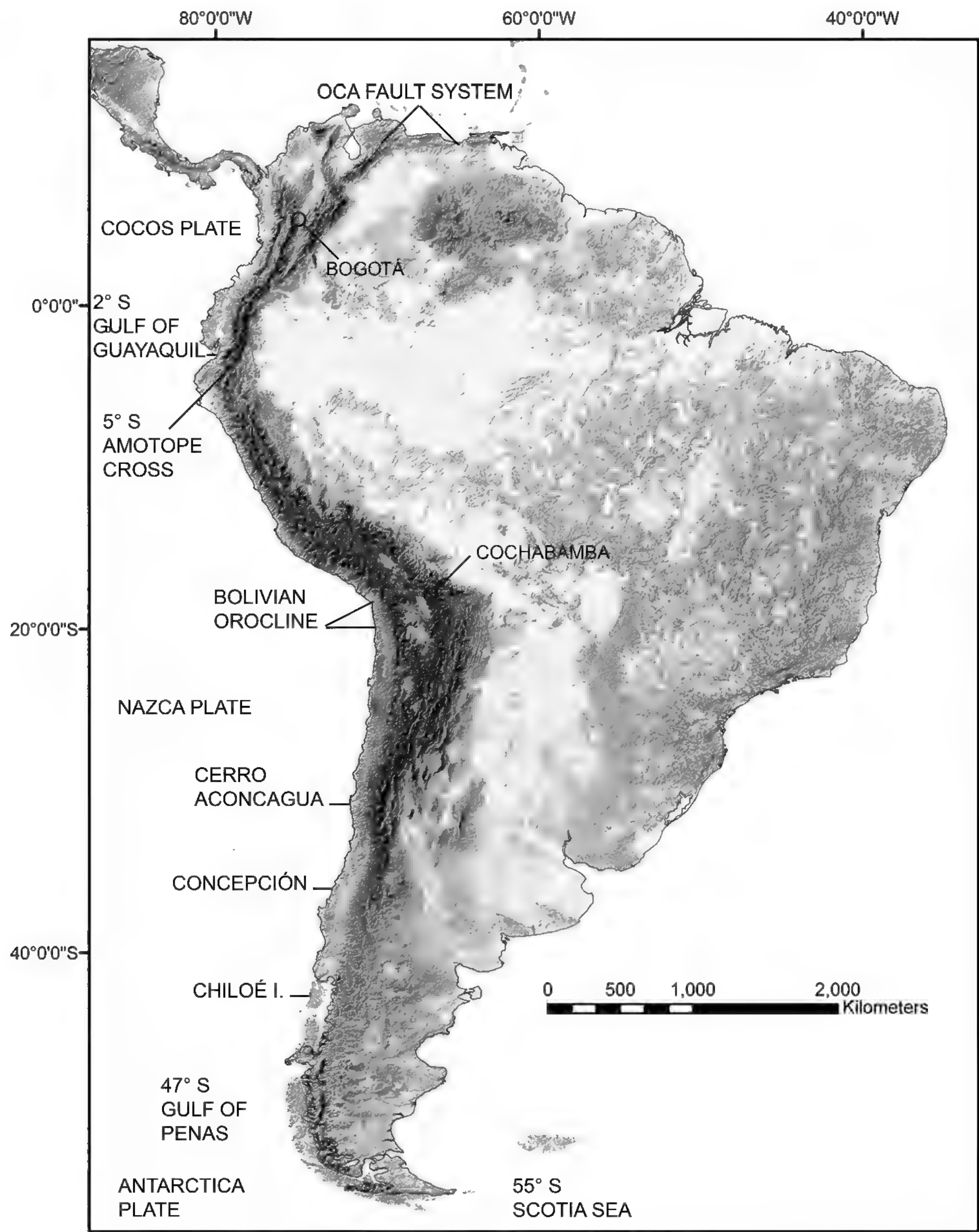


Figure 1. Physiographic map of South America with place names cited in the text using the U.S. Geological Survey Shuttle Radar Topographic Mission 90 m Digital Elevation Data (<<http://srtm.csi.cgiar.org>>).

during periods of mountain building and erosion, while in periods of metamorphism the process runs in the direction of CaSiO_3 and other silicate rocks. That is, more silicate rock is eroded at a faster pace with increased mountain building, resulting in an enhanced drawdown of CO_2 and augmenting the trend toward cooler climates of the Late Cenozoic.

The continuous curve of the Andes extending along the entire length of western South America belies the heterogeneity of the system. An early appreciation of

the complexity and an overview of the processes involved in their formation, ushering in the modern era of geologic studies, were provided by Dewey and Bird (1970). Subsequent investigations documented that various segments of the Andes differ in time of origin, the type and intensity of forces acting on them during various intervals, differential response to these forces depending on the thickness and composition of the rocks, the angle and rate of subduction, availability of lubricating sediments delivered into

the subduction zone (a function of climate), and the variable thickness of the underlying lithosphere. Gansser (1973) suggested the presently recognized subdivision of the mountains into the southern, central, and northern Andes, although some authors recognize seven sections (Moore & Twiss, 1995). These are convenient geographical separations, but they also reflect the varied tectonic forces that have defined the system (Fig. 2).

SEGMENTS AND FORCES

THE SOUTHERN ANDES

The southern Andes extend from the islands off southern South America in the Scotia Sea at 55°S to the Gulf of Penas at 47°S. They are the lowest in average elevation at just over 1 km, and their post-Paleozoic/Early Mesozoic history is slightly older than the mountains to the north, reflecting to some extent the opening of the Atlantic Ocean along the Mid-Atlantic Ridge. The opening began in the south at ca. 120 million years ago (Ma) and progressed northward until South America separated from Africa at ca. 90 Ma at the latitude of eastern Brazil between ca. 0°S and 10°S. Approximately 1 km of uplift in the southern Andes occurred between 17 and 14 Ma (Blisniuk et al., 2006). The peaks there, and the adjacent Patagonian lowlands, were also the earliest to be glaciated. Tills (unsorted glacial sediments) occur interbedded with basalts of Miocene to Quaternary age, and Mercer et al. (1975) found evidence of glaciation by 3.5 Ma.

The principal tectonic forces in the southern Andes are generated by the Antarctic Plate subducting beneath the South American Plate, but the region is also affected by jostling at the triple junction between the Nazca, South American, and Antarctic plates, and it is influenced to some extent by the Scotia Plate. Fragmented lands were accreted to the coast, and subduction of the Nazca Plate, mostly in the Cenozoic and particularly between 50 and 42 Ma and 25 and 10 Ma (Suárez et al., 2000; prior to the 14–10 Ma collision of the Chile Ridge with the subduction zone [Blisniuk et al., 2006]), has acted to pull the coast downward. Relative sea-level rise at various times, including the present interglacial, has contributed further to defining the archipelago extending southward from Chiloé Island (42°S). Recent research suggests that the Late Cenozoic era in the southern Andes has witnessed 18 to 20 glacial advances and retreats, under the influence of the 100,000-year eccentricity cycle of the Milankovitch variations, over the past few million years (Giles, 2005). There are also variations on a finer timescale (see later

discussion). This view of climate change, under a meandering Antarctic anticyclone (high-pressure) system covering an area during the glacial stages double that in the interglacials, and shifting climatic zones northward by 10° latitude, with accompanying fluctuations in sea level and water tables, along with tectonic events, reveal a dynamic physical environment of the southern Andes region, especially in the Late Cenozoic.

The biotic response has been equally dynamic as recorded in numerous spore and pollen diagrams from southern Chile and Argentina (e.g., Heusser, 2003; see summary in Graham, 2009). *Nothofagus* Blume pollen is present throughout most profiles associated with herbs, especially grasses, and there was tundra (*Sphagnum* L., Poaceae, *Acaena* Mutis ex L., Asteraceae, Caryophyllaceae, Cyperaceae, *Empetrum* L.) in the terminal Pleistocene. A grassy steppe developed in the early Holocene (*Chilodactylon* Cass., *Festuca* L., *Mulinum* Pers., *Stipa* L., *Verbena* L.), followed by *Nothofagus* (14,000 years BP) and closed *Nothofagus* forest (10,000 years BP). In the coldest intervals, temperatures are estimated to have been at least 5°C–6°C colder than at present in the lowlands and progressively colder in the highlands, assuming a minimal global average lapse rate of 6°C/km. The earliest occupation of Tierra del Fuego by people was ca. 13,000 years ago (Coronato et al., 1999) as suggested by an increase in charcoal in the stratigraphic records at about this time. The impact of these people on the vegetation, other than by fire, was minimal because they were primarily hunters of *Lama guanicoe* (Miotti & Salemme, 1999).

THE CENTRAL ANDES

The central Andes is the longest segment of the mountain range and comprises 5200 km of the 9000-km length. It is the widest at 750 km and the highest at 3.5–4 km, including Cerro Aconcagua at 6962 m. The central Andes extend from the Gulf of Penas northward to around a megashear zone called the Amotape Cross at ca. 2°S near the Gulf of Guayaquil.

Uplift of the central Andes during the Cenozoic is directly related to the subduction of the Nazca Plate. This plate can be subdivided into as many as seven smaller plates, each exerting related but separate subduction mechanics and each with somewhat different histories. Although it is an immensely complex region, the geology of some portions of the Bolivian section is well known due to two unrelated circumstances. One circumstance is military, dating from a war between Bolivia and Chile (1879–1884) and subsequent border disputes that continue to the present; the other is economic, relating to the

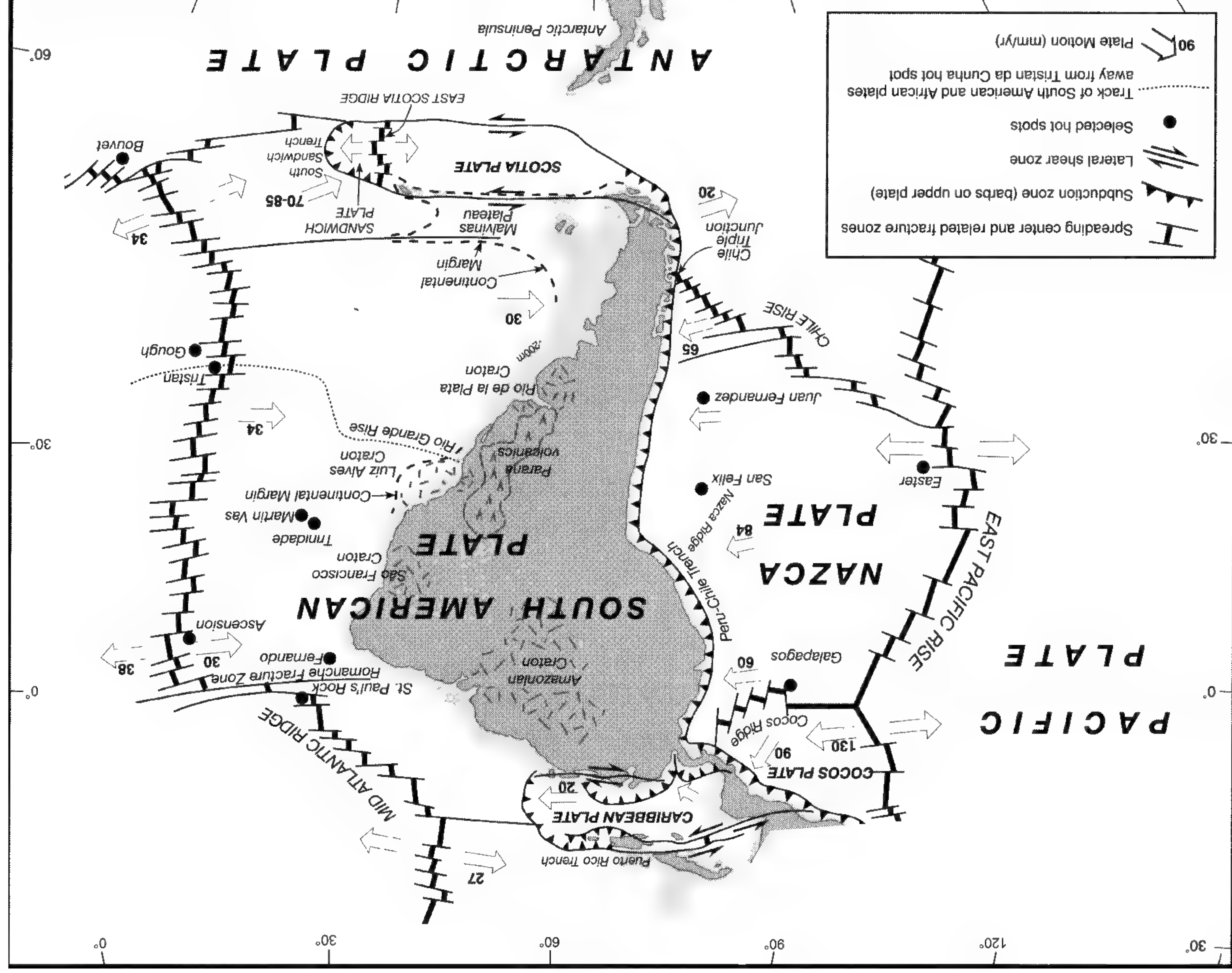


Figure 2. Principal plates acting on South America and the Andes. From Orme (2007a: fig. 1.1, see also fig. 1.2; 2007b: figs. 2.2, 2.4); used with permission of Oxford University Press, Oxford.

extensive deposits of copper, gold, iron, silver, and tin, and the current exploration for oil in the eastern lowlands of Bolivia. These activities have generated topographic and geologic maps, aerial photographs, seismic profiles, satellite images, and collaborative projects between the Bolivian Geological Survey (GEOBOL; Geologic Map Series, 1:100,000 scale) and other organizations. A digital geologic map of the Altiplano and the Cordillera Occidental is available at <<http://geo-nsdi.er.usgs.gov/metadata/open-file/95-494/metadata.faq.html>>, and the economic resources are discussed in a U.S. Geological Survey and Servicio Geológico de Bolivia (1992) publication with an accompanying geologic map. The Cornell Andes Project (<<http://www.geo.cornell.edu/geology/cap/index.html>>) and the Deformation Processes in the Andes Project, a collaborative research program of several German universities and institutes, generate and track information on Andean geology. Lamb (2004) has discussed field experiences involved in obtaining these data in *Devil in the Mountain: A Search for the Origin of the Andes*.

In Bolivia, the mountains consist of three morphotectonic units: the Cordillera Occidental, the 250-km-wide Altiplano, and the Cordillera Oriental (Fig. 3), in addition to the undulating eastern slopes of the Cordillera Oriental called the Yungas. Subduction of the Nazca Plate into the Peru-Chile trench has varied from relatively rapid and steeply angled at ca. 35° prior to the Pliocene, generating volcanism, to a slower, lower-angled, flat-slab subduction of ca. 15° after 5 Ma with less volcanism. The angle of subduction also varies spatially along the Andes from steep-slab subduction in northern Peru and Ecuador to shallow flat-slab subduction in southern Peru and Chile. This helps explain the spatial occurrence of volcanic and nonvolcanic zones in the present Andes. As the subducting plate reaches a depth of ca. 200 km, the leading edge becomes molten and the magma reaches the surface as lava through cracks, fissures, and volcanoes. Some volcanic activity still continues. In January 1835, Charles Darwin saw a “great glare of light” from the eruption of Corcovado Volcano in southern Chile and also observed an earthquake at Valdivia, Chile, that elevated the crust 3 m in a matter of seconds (Darwin, 1845: 277). In May 1960, the largest earthquake ever recorded in South America occurred near Concepción with a magnitude of 9.5 (Richter scale). The last eruption of Llaima was on 2 January 2008 (Associated Press, 2008).

In addition to subduction, which accounts for about one fifth of the height of the Andes, another force is compression generated by westward movement away from the Mid-Atlantic Ridge with the western edge of the continent encountering resistance

against the Nazca Plate and where it encounters eastward-directed force from subduction. Compression accounts for approximately four fifths of the height of the central Andes. A third factor is a thinning of the underlying lithosphere, as in the vicinity of Cerro Aconcagua, which produces heating, weakening, and buckling of the crust to exceptionally high elevations. This thinning often involves the sudden detachment of unstable lower lithosphere and results in a punctuated history of surface uplift (Garzione et al., 2008). In other places, crustal thickening is important, for example, beneath the Altiplano where the lithosphere exceeds 100 km, and these differences in thickness contribute to the differential heights along the Andes.

Once substantial heights have been attained, other mechanisms are necessary to sustain the elevations. If compression was the only force operating on the central Andes, it is estimated they would average ca. 2 km in altitude rather than the actual 4 km. Lamb and Davis (2003) have proposed an explanation that involves changes in climate. The rate of slippage of a plate into a subduction zone depends on the amount of eroded sediments brought in by rivers and that act as a lubricant. If these sediments are absent or curtailed through reduced river flow, subduction slows, friction builds up, and high altitudes are maintained. The development of the cold Humboldt Current, sometime after 30 Ma (opening of the Drake Passage), in combination with altitudes attained by the central Andes that were sufficient to cast a rain shadow to the west at ca. 15 Ma, caused aridity along the coast and minimized transport of sediment into the subduction zone. Compression from the westward drift of South America, combined with greater friction, accounts for ca. 300 km of crustal shortening in the central Andes during the past ca. 35 million years (Sobolev & Babeyko, 2005). Comparable explanations for uplift involving climate have been proposed for the southern central Andes (Alonso et al., 2006) and the southern Patagonian Andes (Blisniuk et al., 2006). Isostasy (rebound of the crust from removal of overlying material by erosion) is another factor.

In the Middle Cretaceous, about 100 Ma, the western border of South America in the vicinity of the central Andes comprised swampland and lakes periodically inundated by marine waters but without substantial highlands. This is shown by the horizontal Cretaceous strata, the paucity of eroded terrigenous sediments, and the presence of shallow-water limestone, including lime and mud with great concentrations of dinosaur footprints. Nearby to the west was a volcanic island arc contributing lava and ash to the Cretaceous sediments.

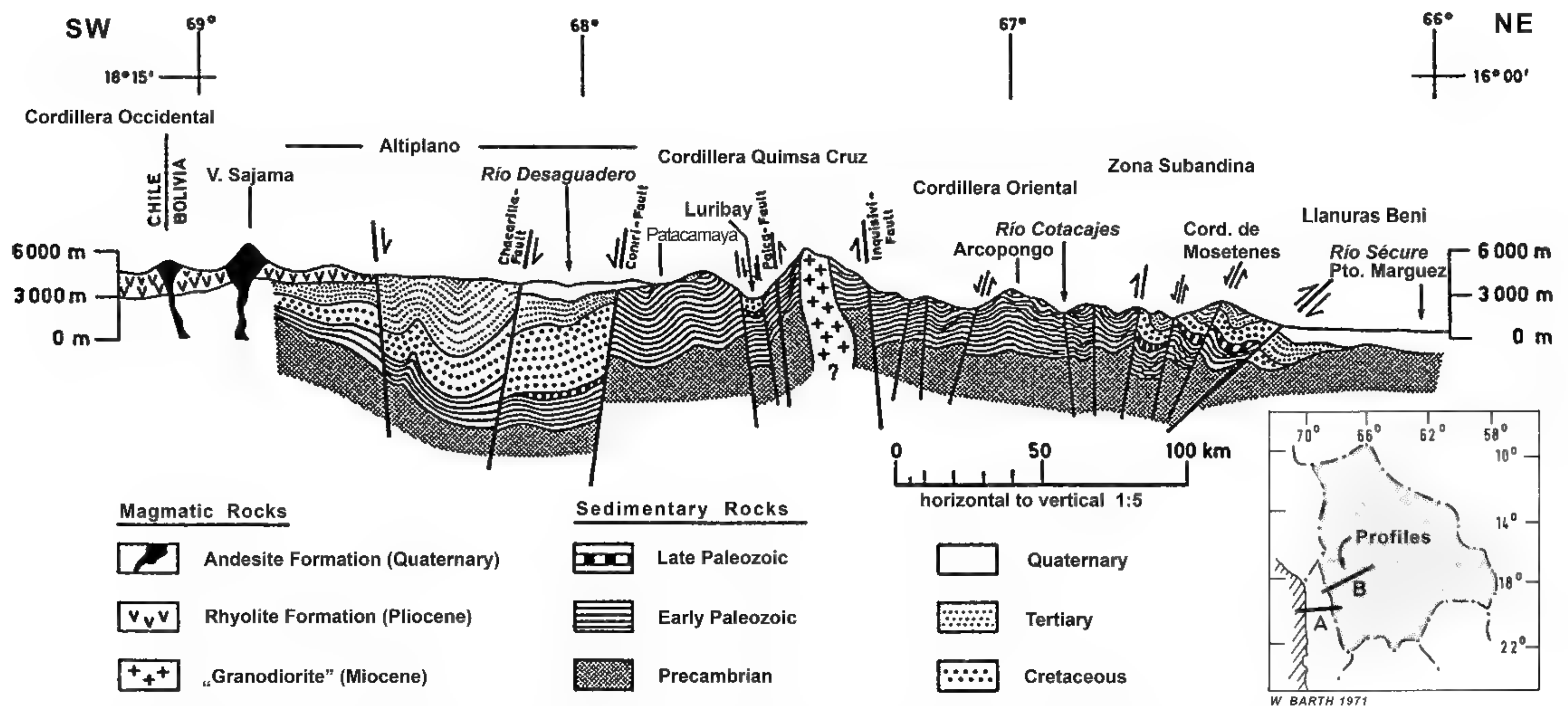


Figure 3. Sectional view of the Bolivian Andes showing approximate elevations, faults, rock types, and ages for the Western Cordillera, Altiplano, and Eastern Cordillera. Note the corrugated topography of the eastern slopes (Yungas) designated Zona Subandina on the figure. From Zeil (1979); used with permission of Borntraeger, Berlin.

Around 40 Ma (Late Eocene), terrigenous sand and silt began covering the swamp, indicating relatively rapid emerging land. One result was deposition of the Potoco Formation that contains a palynoflora of low-altitude terrestrial plants (Horton et al., 2001). Part of the reason for the uplift ca. 40 Ma is that subduction of the Nazca Plate slowed from ca. 15 to 5 cm/yr., possibly due in part to compensation for the intensifying collision of India with Asia at this time (Lamb, 2004: 285). As subduction slowed, sediments cooled and hardened, friction built up, and continuing compression forces resulted in the creation of highlands. This uplift of the central Andes ca. 40 Ma was a biologically important event providing rising uplands where there had been coastal swamps earlier.

By 30 Ma, segments of the line of volcanoes had become appressed to the continental margin, with associated uplift and crustal shortening, notably in the mostly volcanic proto-Cordillera Occidental of southern Peru and Bolivia. The sediments continued to accumulate in the intervening lowlands, which would eventually be elevated as the Bolivian and Peruvian Altiplano. At this time, the Altiplano was a river basin near sea level. Subduction, compression, and appression forces continued, and by ca. 15 Ma (Middle Miocene) approximately half (1500–2000 km) of the present 4000 km average altitude of the central Andes had been attained. Uplift of the Cordillera Oriental also occurred but involved an additional source of compression. As the Brazilian Shield, the original Precambrian craton around which the continent was built, shifted westward subsurface, it underthrust the

Cordillera Oriental. This caused crustal shortening of the Cordillera Oriental of more than 100 km between 30 and 20 Ma, and more than 100 km between 10 Ma and the present, as these mountains rode up and over the western edge of the Brazilian Shield. This contributed to high altitudes and the distinctive corrugated topography of the eastern slopes (Zona Subandina on Fig. 3).

Several paleobotanical studies have contributed to reconstructing the paleoenvironment, vegetation, and uplift history of the central Andes. One is from Pislepampa (17°11'S), 20 km to the northeast of Cochabamba in the Cordillera Oriental of Bolivia at an elevation of 3600 m (Graham et al., 2001). The age of the flora is 6–7 Ma. Among the palynomorphs are spores and pollen grains of *Isoetes* L., *Lycopodium* L., *Cnemidaria* C. Presl, *Cyathea* Sm., *Hymenophyllum* Sm., *Pteris* L., *Danaea* Sm., *Palmae* Juss., and *Cavanillesia* Ruiz & Pav. Megafossils illustrated by Berry (1922) are mostly large and all have entire-margined leaves characteristic of lowland rainforest (bosque amazónico; Killeen et al., 1993). The microfossils also include pollen of *Prumnopitys* Phil. and cf. *Oreopanax* Decne. & Planch., which presently grow together in the cloud forest (bosque húmedo; Fig. 4). The plant fossil evidence indicates deposition near the contact between rainforest and the lower limits of the cloud forest, which is at ca. 1200 m. This implies an uplift of ca. 2400 m since deposition of the Pislepampa flora ca. 6–7 Ma. Other studies on the paleobotany and geology of the central Andes (Gregory-Wodzicki et al., 1998; Gregory-Wodzicki, 2000; Montgomery et al., 2001; Ghosh et al., 2006;



Figure 4. Cloud forest vegetation near Comarapa, Bolivia. The large palmate-leaved plant in the center is *Oreopanax*, and the tall plant to the far right is *Prumnopitys*. The pollen grains are *Oreopanax* (left) and *Prumnopitys/Podocarpus* L'Hér. ex Pers. (right) recovered from the Pislepampa flora (6–7 million years old).

Rowley & Garzione, 2007) suggest an uplift of one third to half the present altitude after 10 Ma; that is, a rise from ca. 2000 m to the present 4000 m. The highest elevation would be the latest achieved, meaning that páramo habitats are the youngest in the Andean system. The latest cooling ushering in the Pleistocene glaciations began in the Late Pliocene, so the combination of maximum altitudes and globally cooling temperatures date the beginning of páramo vegetation to ca. 3–5 Ma, making it the youngest of the Latin American natural ecosystems and affording opportunities for rapid island-like radiation of mid-altitude species (e.g., *Lupinus* L.; Hughes & Eastwood, 2006). Ribas et al. (2007: 2399) attribute existing diversity in montane lineages generally to events in Earth history, and Andean diversity of *Pionus* parrots specifically to three lineages “transported passively to high elevations by mountain building, and that subsequent diversification within the Andes was driven primarily by Pleistocene climatic oscillations and their large-scale effects on habitat change.”

The establishment of a general chronology for the history of the central Andes makes it possible to address two other questions of biological interest. One question is when did uplift reach a point that it constituted a major vicariant event? This obviously varies with the different biotic lineages, their

ecological parameters, and their distribution potentials, although after the Middle Miocene at ca. 15 Ma an increasing number of species to the east and west of the mountains would find it increasingly difficult to interchange.

Another question is when did altitudes of the central Andes of northern Chile, Bolivia, and Peru reach an elevation that rain shadows began forming to the west and contributing to the formation of the Atacama Desert? The gradual separation of Antarctica from South America through the Drake Passage took place between 50 and 30 Ma (Livermore et al., 2005). This event isolated Antarctica from warm marine waters and contributed to the expansion of glaciers and sea ice. The cold Humboldt Current further cooled at about this time, and winds blowing across the water lost moisture and arrived on the western coast as a dry and desiccating wind. A second factor was the barrier to moisture from the east that also developed in the Middle Miocene at ca. 15 Ma as revealed by arid lacustrine (lake) sediments in the forearc regions of northern Chile (Sáez et al., 1999). The Middle Miocene was an important time in the modernization of the Earth's plant communities because Late Cenozoic cooling had reached a stage when water evaporating from the ocean surface became reduced, with an increase in seasonality and

the spread of grasslands and dry forests (Graham, 1999: chapter 7). In western South America ca. 15 Ma, the combination of dry westerly winds and rain shadow allowed elements pre-adapted to aridity from slope, exposure, and edaphic conditions, as well as from immigration, to coalesce into the beginnings of an ecosystem recognizable as desert.

Among the myriad features of the Andes relevant to the biology of the region is the Bolivian Orocline or “elbow of the Andes” at ca. 18°S. Killeen et al. (2007) suggested that this bend presents a face more at a right angle than other sections to winds coming off the Amazon Basin and augments rainfall on the already wet lower slopes. If so, this may have perpetuated wet conditions during dry intervals of the Late Cenozoic and served as a refugium for rainforest taxa (see discussion in Graham, 2009: chapter 8). Another physical feature of biological interest is the east-facing concave, almost semicircular shape of the Andes toward the Amazon between ca. 8°S and 10°N. This feature traps humidity and further augments wet conditions on the slopes and in the lowlands.

A focus of current environmental and vegetation history studies in the central Andes is on the Quaternary period of the Altiplano. In the northern Altiplano around Lake Titicaca (Baker, 2001a, b; Paduano et al., 2003; Tapia et al., 2003), temperatures were estimated to be 3°C–5°C cooler than at present until 21 thousand years (Kyr) BP (around the late glacial maximum) and the snow line was ca. 500 m below the current 4850 m. Then a warming trend began with higher lake levels and wet conditions until ca. 10 Kyr BP, followed by a mid-Holocene warm dry period (9000–3100 years BP, especially between 7960 and 3100 Kyr BP) when water levels dropped by 100 m; salinity, charcoal, and dust levels increased; and temperatures were an estimated 1°C–3°C warmer than at present. At the Salar de Uyuni on the Altiplano, moisture may have varied with Heinrich events 1 and 2 and with the Younger Dryas cold event between 13 and 11.5 Kyr (Baker et al., 2001a; see below). Lakes started to rise at ca. 4000 years BP and reached modern levels at ca. 1500 years BP (Abbott et al., 1997a, b).

In the southern Altiplano, at the upper limits of the Atacama Desert, Placzek et al. (2006, 2009) include 53 new uranium-thorium (U-Th) and 87 new ¹⁴C dates that provide a more precise chronology for climate change. The basins or salars are now mostly dry, and the region is a barren and rocky landscape of lava, shifting dunes, and some of the largest salt flats on Earth. However, between 120 and 98 Kyr BP there were lakes 80 m deep on the Altiplano. These intermittently shallowed between 98 and 18.1 Kyr BP, then at 18.1–14.1 Kyr BP, a lake ca. 140 m deep

developed that was the largest and deepest of the past 120 Kyr (Placzek et al., 2006). Subsequently, there were smaller changes on a finer timescale that reflect climatic fluctuations of the Holocene. The moister intervals and higher lake levels correspond to periods of human occupation on the Altiplano, whereas during the driest intervals (e.g., 9500–4500 years BP) the sites were abandoned (Grosjean, 1994; Grosjean & Núñez A., 1994; Núñez et al., 2002; Grosjean et al., 2005).

THE NORTHERN ANDES

The northern Andes extend from 5°S at about the Amotape Cross at 2°S to the Oca, Romeral, and other fault systems across northern South America at the contact with the Caribbean Plate at ca. 12°N (Fig. 5). The Andes branch in southwestern Colombia to form the Cordilleras Occidental, Central, and Oriental (Orme, 2007a: fig. 1.5). The Cordillera Oriental branches again into the western Sierra Nevada de Santa Marta and Sierra de Perijá and the eastern Cordillera de Mérida, the two branches enclosing Lake Maracaibo. The latter is a region of major petroleum reserves and, like the mineral deposits of the Altiplano, it has been the impetus for numerous geological, paleoenvironmental, and vegetational history studies (Germeraad et al., 1968; Jaramillo & Dilcher, 2001). The Andes continue along the northern coast as the Caribbean Mountain system with portions submerged to form the Netherlands Antilles and other islands of the southern Caribbean Sea.

The northern Andes are as complex as the central Andes, but their uplift and other features are due to a different combination of tectonic forces (Kroonenberg et al., 1990). In the Late Cretaceous, there was some restriction between the Amazon Basin and the Pacific Ocean, but passages existed through which the proto-Amazon and proto-Orinoco rivers drained into the Pacific. During the Paleocene, marine sediments were still being deposited at sites in the present northern central Andes (Sempre et al., 1997). By the Middle Miocene (ca. 15 Ma), the mountains had reached sufficient height so that there was substantial warping, ridging, and some tilting of the Amazon Basin eastward, and the rivers started to flow toward the Atlantic Ocean. Evidence for the timing of this event comes from varied sources. Van der Hammen (1952), Hoorn (1994a, b, 2006), and Hoorn et al. (1995) note a change along the Solimões River from west-dipping cross-bedding (Mariñame unit) to east-dipping cross-bedding (Solimões and Pebas formations) between the Early and Late Miocene. A submarine fan first appears at the mouth of the Amazon River in the

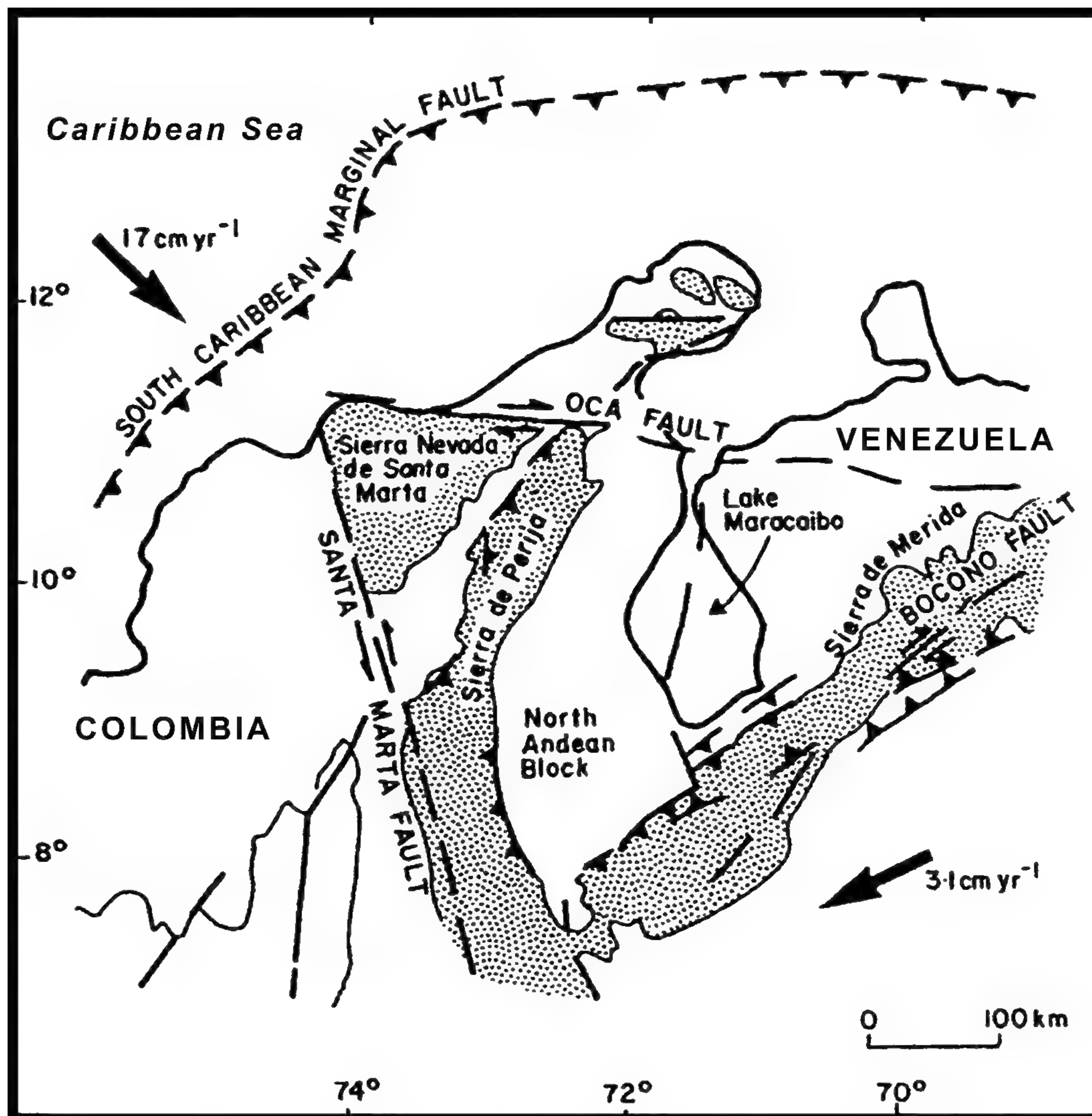


Figure 5. Portion of the North Andean Block in eastern Colombia and western Venezuela, including the Santa Marta Block and the Perijá and Merida Andes, with principal structural features. From Clapperton (1993); used with permission of Elsevier, Amsterdam.

Middle Miocene, and delta deposits of the same age begin to form along the coasts of the Guianas.

The tectonic factors include subduction from the Nazca Plate beneath northwestern South America at a present rate of 3–6 cm/yr., with a particularly complicated section at the junction with Cocos Plate. There is compression from the westward movement of the continent against the plate, shearing along the northern coast as South America moves westward relative to the Caribbean Plate, and appression that has brought volcanic island arcs and terranes onto the northwestern coast. One of these is the Cordillera Occidental, which is composed of accreted terranes of

volcanic origin, while the Cordillera Oriental and Cordillera Central are primarily nonvolcanic mountains. The proto-Cordillera Occidental was accreted onto the coast in the Late Cretaceous (Winsemann, 1994) as indicated by a line of ophiolites (oceanic basalts caught between suturing plates). By the Middle to Late Miocene, the northern Andes were about half their present average elevation, which is slightly later than the southern Andes. Uplift of the Cordillera Oriental to its present height occurred between 6 and 3 Ma, and it is estimated that the Sierra de Perijá has risen 11–16 mm/yr. since the Late Pliocene (Clapperton, 1993).

The rise of megamountain systems has many effects on the immediately surrounding region. In the Late Miocene, uplift of the Cordillera Oriental of the northern Andes blocked the flow of the Maracaibo River and formed Lake Maracaibo. This event created conditions favorable to the formation of extensive oil reserves in the basin where the need for accurate stratigraphic correlation, zonation, and environmental reconstruction resulted in extensive palynological studies by the Bataafse Internationale Petroleum Maatschappij (later Shell Oil), and the publication of the first extensive survey of Tertiary vegetation from the tropical areas of South America (Colombia, Venezuela, Trinidad, the Guianas; Germeraad et al., 1968). The work is still of systematic, biogeographic, and paleoecologic value, because microfossils were identified according to their biological affinities rather than by an artificial stratigraphic nomenclature.

Paleodrainage patterns in the Amazon Basin, and changes in these patterns induced in large measure by the rise of the Andes Mountains, are important because they fragment the biota into geographically and thereby reproductively isolated populations. Deltaic deposits allow tracing the meandering course of rivers through long intervals of time. In the Middle Eocene, the Misoa paleodelta identifies a large river flowing north into the Maracaibo Basin that drained the Cordillera Central and the Guyana Highlands. Uplift of the mountains shifted delta formation southward as shown by the Late Eocene to Oligocene Carbonera Formation in the Llanos Orientales region of Colombia and Venezuela. By the Middle to Early Miocene, there was a delta in the northwestern part of the Falcón Basin to the east of Maracaibo, and in the late part of the Middle Miocene it had shifted to its present position in the Venezuelan Basin south of Trinidad and Tobago (Díaz de Gamero, 1996). These record the positioning of the Amazon and Orinoco rivers between the Late Eocene and the Middle Miocene, and similar changes affected all the rivers and tributaries in the Amazon and Orinoco basins during the Tertiary.

Alfred Russell Wallace (1849, 1876) used these river drainage patterns to develop his riverine hypothesis that maintained the past and present distribution of species in the Amazon Basin has been strongly influenced by river barriers, and this has generally proven to be true, especially for mammals such as the tamarinds. For other animals, such as some rodents, other factors were involved, and these were the result of the uplift of the northern Andes. Patton et al. (1994; Patton & Da Silva, 1998, 2005) found that some populations, although morphologically similar, differed in having distinct mitochondrial DNA (mtDNA) signatures. The populations were not

segregated on different sides of the most obvious barrier, the Juruá River, but rather between the upper reaches and the mouth of the river. Patton (quoted from Morell, 1996: 1497) noted that "What is really striking ... is that all 11 [of the 17 species] are separated at almost the same geographical point on the river, although there is nothing remarkable about the spot—no bend, no hill, no valley." The demarcation is at the ancient Iquitos Arch, which is one of several arches formed during mountain uplift and that subdivided the basin into a number of subunits. The basin floor is now covered in places by more than 4000 m of eroded sediment that obscures the arches, but they were once effective barriers to the interchange of some groups of organisms, and this history still resides in their molecular signature. The arches also affect the distribution of sediments and, thereby, edaphic patterns in the Amazon Basin (Dunne et al., 1998).

Another effect of Andean uplift, combined with sea-level changes and subsidence of the basin from sediment accumulation, was the periodic drainage and inundation of the basin by marine or brackish water (Hoorn et al., 1995), primarily from the Caribbean Sea through the Maracaibo Basin. Fish faunas and mangroves are good indicators of the time and extent of the flooding when the biota are fragmented and reunited. The ichthyofauna reveals several such flooding events in the interior, persisting until the Late Miocene, as well as periods of deeper or shallower, and possibly torrential waters (Monsch, 1998). The Amazon Basin includes the greatest number of freshwater fish species in the world, and Lovejoy et al. (1998), on the basis of the molecular phylogeny of stingrays, believe that this diversity resulted from the repeated fragmentation and reassembly of populations through intervening brackish or salt water. Volcanic ash deposits in eastern lowland Peru contain paleofaunas from 9.01 Ma and 3.12 Ma (Campbell et al., 2001), and the latter date marks the last marine incursion around the margins of the basin.

In other mountainous volcanic settings, there is evidence of the impact of local orogenic history on speciation patterns. On Isla Isabela in the Galápagos Islands, five taxa of the large tortoise occur, one on each of the five volcanoes of the island. *Geochelone nigra vandenburghi* on Alcedo Volcano has considerably less matrilineal diversity in its mtDNA. Although all the volcanoes are about the same age (ca. 500,000 years), Alcedo Volcano last erupted ca. 100,000 years ago. The suggestion is that the event drastically reduced the population diversity from which this particular lineage was derived (Beheregaray et al., 2003). Similar reductions may have occurred among other slow-dispersing organisms isolated in mid- to

Table 1. Glacial/climatic events first discovered in the Northern Hemisphere and now recognized in South America.¹

Location	Glacial/climatic event	Reference
Venezuela (9°N–10°N)	Younger Dryas, mid-Holocene warm/dry period, Little Ice Age	Haug et al., 2001
Colombia (4°N–5°N)	Younger Dryas	Thouret et al., 1996; van der Hammen & Hooghiemstra, 1995
Brazil (3°N–4°N)	Younger Dryas, Heinrich and Dansgaard-Oeschger events, Little Ice Age	Jennerjahn et al., 2004; Cohen et al., 2005
Ecuador (3°S–4°S)	Younger Dryas	Osborn et al., 1995; Heine & Heine, 1996; Clapperton et al., 1997
Peru (8°S)	mid-Holocene warm/dry period, Little Ice Age	Osborn et al., 1995
Bolivia (15°S)	Younger Dryas, mid-Holocene warm/dry period, Heinrich events 1 and 2	Osborn et al., 1995; Abbott et al., 1997a, b, 2000
Chile (Lake District; approximately 30°S–42°S)	Younger Dryas, Heinrich events	Lowell et al., 1995
Southern Argentina–Chile (Patagonia; 45°S)	mid-Holocene warm/dry period, Younger Dryas, Little Ice Age	Mancini et al., 2005

¹ Arrangement is from north (Venezuela, 9°N–10°N) to south (southern Argentina–Chile [Patagonia], 45°S). Evidence for the Younger Dryas in the tropical Andes is considered equivocal by Rodbell and Seltzer (2000) and Seltzer (2007).

higher-elevation habitats along the volcanically active Andes where comparable studies could be made.

Within the mountains, there are many basins now filled with eroded sediments. The high plain of Bogotá is the floor of a drained lake. The Bogotá Basin formed ca. 6 Ma when the Cordillera Oriental was beginning a period of major uplift. It was raised to its present altitude of 2550 m between 4 and 3 Ma, with almost continuous sedimentation since then. The Bogotá Basin has been the site of important paleoenvironmental and vegetational history studies beginning with those of van der Hammen (e.g., van der Hammen et al., 1973) and continuing with those of Hooghiemstra (1984) and Hooghiemstra et al. (2006). Among the results has been the early recognition of downward shifts in high Andean vegetation during cold intervals that were suspected to have affected the lowland Neotropical rainforest. Later studies have shown this to be true (e.g., Hooghiemstra & van der Hammen, 1998; van der Hammen & Hooghiemstra, 2000). Another result was the demonstration of climatic changes and vegetation responses throughout the entire 3.5 million year interval represented by the basin sediments. Some of these correlate with regional to global events elsewhere (e.g., the Younger Dryas; see below).

Quaternary climatic and vegetation changes throughout the Andean chain are important for interpreting the regional vegetation history, but they have broader implications for environmental changes throughout South America. Many of the temperature and precipitation patterns of the Quaternary were initially documented in the northern latitudes and especially around the North Atlantic Ocean. In addition to the longer-term fluctuations of 100,000,

41,000, and 23,000 years of the Milankovitch variations (with subcycles), there were warm and cold intervals on a much finer scale. These intervals include the cold reversal during the terminal Pleistocene/Holocene called the Younger Dryas (13,000–11,500 years BP), the Medieval Warm Period (800–1200 CE), and the Little Ice Age (1300–1850 CE). Heinrich events are cold periods of a few to several thousand years' duration, while Dansgaard-Oeschger (D-O) events occur on a scale of a few thousand to several hundred years. These events involve fluctuations in the thermohaline (conveyor belt) transport of heat in the form of warm surface waters from the tropics to the North Atlantic; cooling of these waters; and transport back to the tropics as cold Atlantic deep water, where it warms and returns again northward.

When results of the Climate: Long-range Investigation, Mapping, and Prediction project (CLIMAP, 1976, 1981, 1984) and the Cooperative Holocene Mapping Project (COHMAP, 1988) were published, they suggested that while temperatures were colder by 12°C–14°C in the high northern latitudes at the Last Glacial Maximum, equatorial temperatures remained the same or cooled by a maximum of ca. 2°C. The work previously cited for the High Andes was difficult to reconcile with the climatic and the implied vegetation stasis of the tropics, but definitive evidence was not yet available. Then Grimm et al. (1993; Watts & Hansen, 1994) found fluctuations in pine pollen that corresponded with Heinrich events 1 to 5 in bogs at Lake Tulane, Florida (28°N). Guilderson et al. (1994) proposed a lowering of 5°C at the Last Glacial Maximum based on strontium:calcium ratios from corals on Barbados at a latitude ca. 12°N, and several

studies now document a similar cooling for the Brazilian lowlands (Stute et al., 1995; Webb et al., 1997; Aeschbach-Hertig et al., 2000). There is now paleobotanical and independent geologic evidence for rapid temperature and precipitation changes from several places in the tropics (Table 1; see Graham, 2009 for additional references).

One reason these kinds of evidence are significant is that for a long time, through about the 1960s, it was thought that tropical climates and the tropical biota were stable and unchanging (e.g., Corner, 1958). This seemed to be supported by the CLIMAP (1976, 1981, 1984) and COHMAP (1988) results of the 1970s and 1980s. In turn, this could be used to rationalize the view that the tropical biota could be impacted with impunity and would recover because they had endured unchanged for millions of years. This was suspected not to be true (see reviews, e.g., by Vuilleumier, 1971), and a study of the mid-Pliocene Paraje Solo microfossil floras in southern Veracruz, Mexico, provided direct paleobotanical evidence that in an area where rainforest is the dominant vegetation today, it was not present in the recent geologic past (Graham, 1976a, b). Subsequent studies have extended this finding to other communities and other locations, so that today all ecosystems throughout the equatorial latitudes, from lowland rainforest to the páramo of the High Andes, and from Brazil, Colombia, and Venezuela to Argentina and Chile, are recognized as delicately balanced assemblages that have taken millions of years to develop, have had a dynamic past on all timescales, and deserve the conservation and sustainable development efforts that fact alone implies.

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